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THE ANNULUS OF A MEXICAN CRAYFISH.

E. A. ANDREWS.

It is well known that the females of the common American crayfishes of the genus *Cambarus* possess a peculiar structure called in systematic descriptions the "annnlus ventralis." In our common northern crayfishes it has been shown (1) that the annulus contains an essential accessory reproductive organ, the seminal receptacle, without which the species would become extinct. Ortmann has recently divided the genus into six subgenera (2) and also (3 and 4) given reasons for supposing that the seventy or more species of *Cambarus* now living in the United States and adjacent territory are descended from forms once living in the region now called Mexico. As some of the more primitive subgenera are found only in Mexico and as it is not known whether the annulus in any Mexican crayfish contains a reproductive organ or not it seems worth while to describe the real character of the annulus in any Mexican crayfish that can be obtained.

The question as to the evolution and spread of the genus *Cambarus* cannot be completely answered till it is shown that the annulus in all members of the genus does contain the sperm receptacle, and that they thus differ from all other crayfish the world over.

The crayfishes whose annulus is here described were bought in the market of the city of Mexico, in July [1] and prove to be *Cambarus montezumæ* Saus. of the typical form.

This species was first described in 1857 by Saussure (5), but

[1] These specimens were obtained by Horace Andrews, C.E., with the aid of W. W. Blake. They were on sale, cooked, as taken in Lake Zumpango and known by the Astec name "Acociles."

without mention of the annulus; subsequently Martens (6) described a variety and Faxon (7) gave a new account of the typical form, of which he says the annulus "is movable, fixed only at the posterior end, between the sterna of the penultimate and last thoracic somites. The ventral face of the annulus is marked by a longitudinal fossa open at the posterior end" (page 122). Several varieties of the species were later briefly described by the same author (8). Recently Ortmann has examined the specimens of Mexican crayfishes from the Paris Museum (2) and mentioned in a footnote that the peculiar spine posterior to the annulus in his new subgenus *Paracambarus* distinguishes this from all other Cambari except *C. montezumæ*.

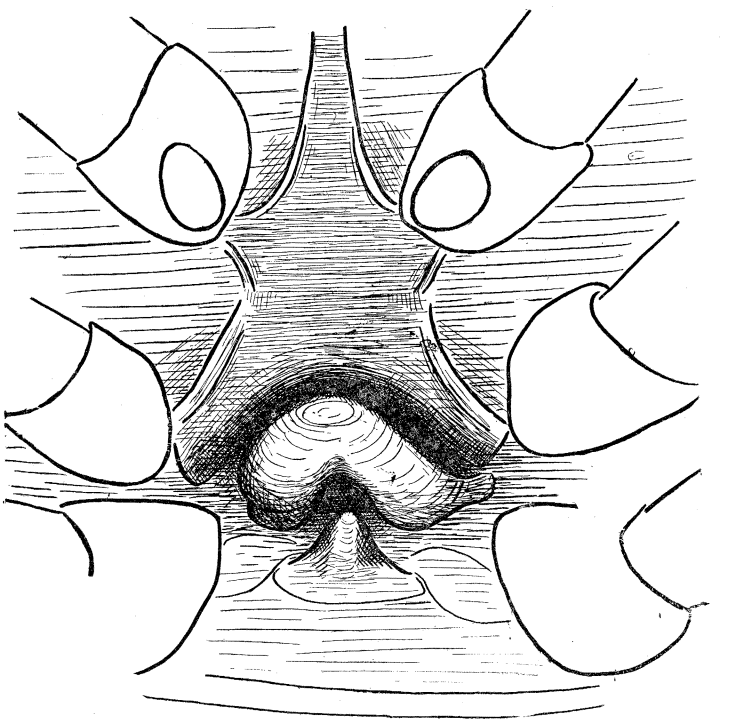

FIG. 1.

The above is all thus far known regarding the annulus in *Cambarus montezumæ*, or in the subgenus *Cambarellus*, in which it is placed by Ortmann.

Of the 179 specimens sent to me 88 were females ranging in length from 16 mm. to 36 mm., many being 25–28 mm. The males ranged from 14 to 36 mm. and many were 25 mm. Saussure had 25 specimens, which measured up to 27 mm., while Faxon's largest was 35 mm. That those 30–36 mm. were sexually mature was evident from the fact that six bore eggs, and two, young larvæ, attached to the abdominal appendages, as in other crayfishes.

The general appearance of the annulus in these small, but mature forms is indicated in Fig. 1, which shows the bases of the third to the fifth thoracic legs and the sternal surface between them. While the annulus has the same position as in all other Cambari, between the sterna of the fourth and fifth legs, it differs from any hitherto figured in not being a low transverse plate of more or less annular form but in forming a high transverse papilla of asymmetrical form.

The sternum between the fifth legs is also more specialized than in higher Cambari in that it projects as a stiff spine, somewhat like a lengthwise ridge, but often more like a conical spine.

This spine fits into a very marked median groove on the posterior side of the annulus in the manner mentioned by Ortmann (2) as characteristic of his new form, *Paracambarus paradoxus*. The eggs issuing from the elliptical openings on the third legs (Fig. 1) doubtless flow back around the base of this rounded, papilla-like annulus, and there receive the fertilizing sperm, for we find in this annulus a functioning sperm receptacle.

The appearance of the annulus when cut off and viewed from the posterior side is shown in Fig. 2. The right and left of the high papilla are unevenly balanced about the long deep median groove and on the observer's left, which is the animal's right, there is a peculiar structure, which proves to be the seminal receptacle. The asymmetry of the annulus is marked, the apex being to one side and the side containing the receptacle being abrupt while the opposite one slopes gradually.

In the crayfish hitherto studied the receptacle is wholly, or in part, on the median line but here we find it entirely to one side. In those crayfish there is, as far as studied, a peculiar dimorphism amongst the females (9), some of them having the entrance of the

receptacle on the right side of the body and some on the left. In this Mexican crayfish it is surprising to find that the dimorphism

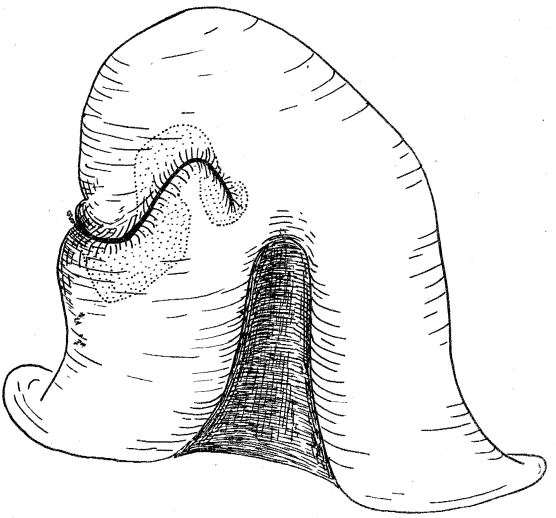

FIG. 2.

is expressed by a transposed position of the entire receptacle. As it happened just forty-four of the females had the receptacle on

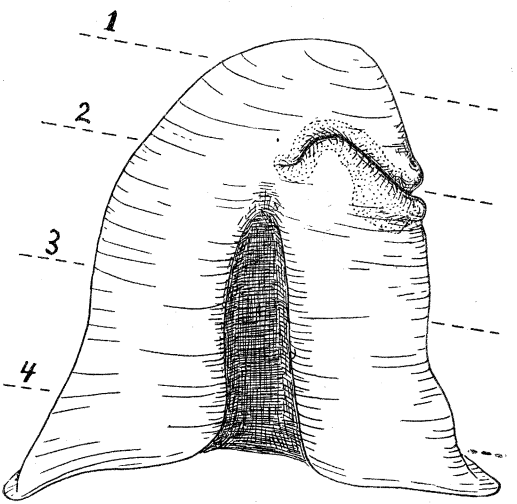

FIG. 3.

the right as in Fig. 2 and the other forty-four on the left. In these left-handed females the posterior side of the annulus appeared as in Fig. 3. Leaving out of account the differences in height and width and the altitude of the receptacle, which are diverse in individuals either dextral or sinistral, the annulus in Fig. 3 is the mirror image of that in Fig. 2 : the abrupt and the slop-

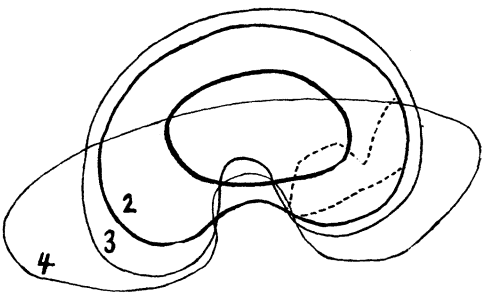

FIG. 4.

ing sides and the position of the apex are reversed and this is obviously associated with the fact that the receptacle is on opposite sides in the two cases.

The real shape of the annulus in either sinistral or dextral forms is seen only after observation from different points of view. The annulus is wide from side to side and compressed from before back, very protuberant in front and less so behind and has a very small base, which accounts for the movability noticed by Faxon. A view of the sinistral annulus (Fig. 3) taken from the side that bears the receptacle is shown in Fig. 5, which emphasizes the very narrow base and the greatly protruding anterior face. The apex is also seen to rapidly taper. The receptacle obviously extends around onto this lateral side above the level of the central groove, which is indicated in broken lines as seen through the side. Upon looking down upon this same sinistral annulus

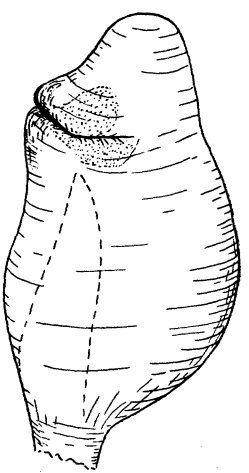

FIG. 5.

from above, successive optical sections presented the outlines seen in Fig. 4: the heavy black line is the outline of the apex above the receptacle; the line No. 2 is the circumference of the annulus around the level (2) of Fig. 3, and in the receptacle is represented by dotted lines; the line 3 shows the maximum thickness from before back, also the greatest depth of the median groove; finally the line 4, Figs. 3 and 4, shows the great width of the annulus and its compression from before back, near its base. An anterior view of this same annulus was like Fig. 3 but with the sides reversed and with the annulus and median groove invisible until the annulus was made transparent, when they were seen through its substance.

By study of annuli cleared whole and also cut into sections the internal structure was seen to agree with what was made out for other annuli (9). Thus a lengthwise section (Fig. 8), shows a thick exoskeleton lined by nucleated epidermis and a central mass of areolar connective tissue full of blood sinuses and vessels with no discovered musculature. The shell on the straighter posterior face seems thicker than on the more protuberant anterior face. The infolding near the upper end was the part of the receptacle of this dextral annulus, cut near the right face.

As a protruding mass of connective tissue covered with thick exoskeleton the annulus in other crayfishes forms a stiff plate more or less movable since the exoskeleton round about it is less thick and more pliable, but in *Cambarus montezumæ* the mobility is apparently enhanced from the fact that the great height of the mass and its narrowed base make it easy to rock it back and forth. The convex front face of the annulus fits against the hollowed out sternal plate of the somite bearing the fourth legs, as s imperfectly indicated in Fig. 1.

As the spine on the middle of the sternum behind the annulus is on that somite of the thorax which can be independently moved by the animal, it may be that the annulus is sometimes caught between the spine that enters its posterior groove and the solid sterna in front of it and subjected to pressure and this may be a means of emptying the receptacle.

The receptacle itself proves to be made precisely along the same lines as in the other crayfish in which it has been described

(9): it is a rather simple infolding of the epidermis, lined by the exoskeleton and is a mere flat pocket opening to the exterior by a narrow chink.

The mouth of the sperm pocket is the sinuous line seen in Figs. 1, 2, 3 and 5, passing as an S-shaped line from the neighborhood of the median groove to the right or the left as the case may be, across the posterior face and then around onto the lateral face of the annulus. It is not extended onto the anterior face. For most of its extent the line is a closed suture, or mere morphological mouth, forming a chink that is apparently closed up, but toward the edge of the posterior face and on the lateral face the chink is more patently an opening into the interior. The lips of this suture are more or less swollen especially on the lateral face and toward the edge of the posterior face and this is much more pronounced in some individuals than in others (Figs. 2 and 3).

The internal pocket into which the suture leads may be seen through the exoskeleton when properly prepared and, as indicated in the above figures by the dotted areas, it extends out rather far on either side of the suture in a peculiar way.

A good idea of the shape of the internal pocket may be got by looking at it from the inside, as in Fig. 6, that is, by removing the anterior walls of the annulus and all the connective tissue and epidermis; the exoskeleton that lines the sperm pocket stands forth as a prominent ridge passing sinuously from side to side. Fig. 6 is such an anterior view of the exoskeleton of the sperm-pocket of a right-handed annulus, similar to Fig. 2. The flat, sinuous ridge there indicated is attached all along the posterior side of the annulus and free anteriorly, toward the observer; the part to the right is the beginning of the pocket on the lateral face of the annulus and stands forward as do the middle and the left parts, forming three roughly parallel parts of an S.

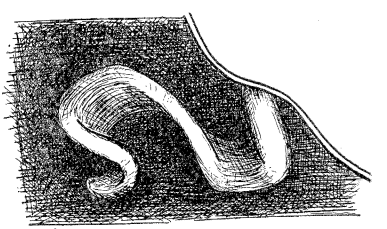

FIG. 6.

The extreme tip to the left, as well as two intermediate regions, are lower and are bent alternately down, up and down. Thus one sees on the right only the top of the ridge, then part of its upper or distal surface, then the top, then part of its lower or proximal surface, then the top again and finally the upper surface at the end. By this mode of bending as a warped surface the edge of the pocket, or ridge, toward the observer is longer than the anterior edge, which is the mouth, so that the same condition is found as in higher crayfish and the sperm pocket is like an elastic coat pocket which should have its mouth bent in an S and its bottom pulled out into an S with longer loops, after the fashion of a mesentery that has a shorter origin and a longer line of attachment. Seen on the outside (Figs. 2 and 3) this greater bending of the internal than of the external

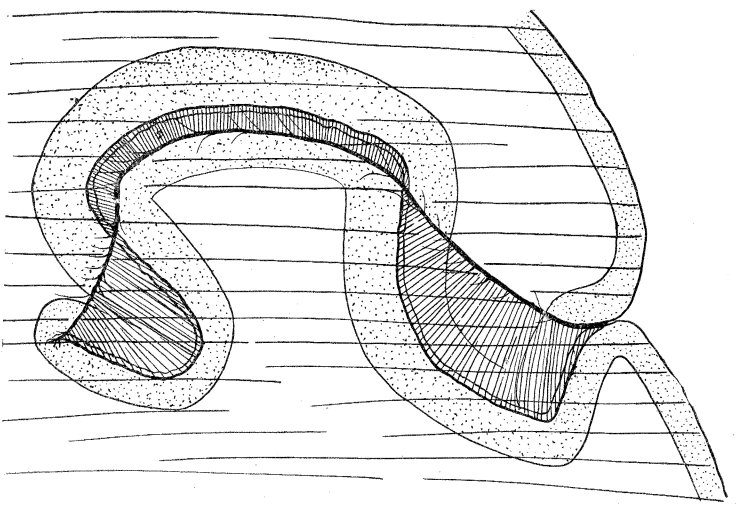

FIG. 7.

limiting edge is evident and variable. In old well-marked annuli the pocket (Fig. 2) drops down from its mouth in a long sweep toward the base of the annulus and then sweeps up above the suture toward the summit to return again toward the median end of the suture. In other cases (Fig. 3) the pocket is less drawn out toward the summit and stands more at right angles to the surface. When more magnified such a receptacle seen from the

outside as a translucent object is represented in Fig. 7. The line of the mouth coming around from the left face makes an imperfect S which is much shorter than the inner edge of the pocket walls, indicated as a continuation of the outside shell. Through the thick exoskeleton runs only a narrow crevice the outer mouth of which is shown as the black line or suture and the bottom of which is indicated by two parallel lines which cross the suture at two points. The sides of the chink, or cavity of the pocket, are diagrammatically represented by ruled lines. The cavity of the pocket thus runs in from the mouth at first obliquely downward and to the observer's left then slightly upward and then downward again and toward the observer's right.

In other cases (Fig. 10) the middle loop toward the apex of the annulus is much more pronounced. The simple nature of

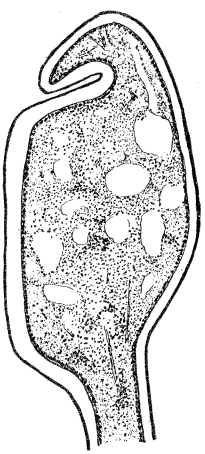

FIG. 8.

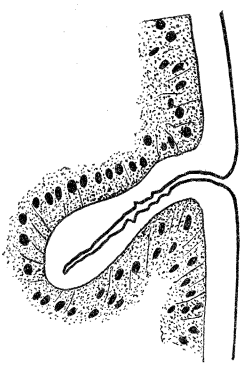

FIG. 9.

the pocket is shown in the lengthwise section of the annulus (Fig. 8) which shows the narrow cavity of the pocket of a dextral annulus near its origin toward the right face of the annulus.

Other sections show the same simple pocket, whenever cut at right angles to its twisting course. In Fig. 9 is shown, enlarged, the terminal part of a dextral pocket cut near its median termination where it slopes away from the surface toward the median plain and also down toward the base of the annulus. Here as elsewhere the pocket is seen to be really an invagination of the

epidermis lined with exoskeleton that has the same shape. By careful dissection this epidermis was removed in other cases as a hollow mould in which the exoskeleton had fitted.

That this thin, flat slit in the shell of *Cambarus montezumæ* actually is used as a sperm reservoir is well proven on two specimens that show the sperm as it was issuing out of the mouth of the pocket. One of these (Fig. 10) was a dextral annulus like Fig. 2. In this figure the bottom of the pocket is represented by dotted parallel lines and the exoskeleton by parallel rulings. The outer mouth or suture is shown as a black line. Extending out from this on its middle loop is a large area covered with dots and these were round, flat, clear bodies which with 6 and 2 mm. objective clearly showed the characteristic central bowl of crayfish spermatozoa. These sperms were issuing out of the middle loop of the suture and spreading on either side over the surface of the annulus where they might meet the eggs (Fig. 1). The sperm seemed to be in a single layer over a considerable area, though in a deeper mass where emerging from the suture. They lay flat side by side and their clear outer part around the central bowl suggested that they might be gliding along somewhat like a liquid wetting the annulus. No radiating arms were made out, so that here again the male must have succeeded in transferring the sperm into the annulus without the expansion of the sperms into those stars which were so often produced by the liquids used by investigators as to be regarded as the only shape of the mature sperm. The part played by the male must be the same as in other Cambari for an examination of the first male pleopods revealed some of these same round sperm cells issuing out of the tip of the "canula" or discharging tip of that appendage, which is doubtless inserted into the receptacle.

Whether the above figured sperms were forced out at the time the animals were killed, or just before, is not known, but the appearances are that pressure of some kind must be applied not only to get the sperm into such a stiff rigid pocket (Fig. 9) but also to get it out again. In another specimen the sperm had issued out of the suture all along its median as well as its middle loop and this was probably the case in Fig. 10 before it was examined.

In both cases the first loop of the suture showed the thin plate of wax-like material represented in Fig. 10 as the darkened mass along the first curve of the suture. This wax also projected on the lateral face as the "sperm plug" so much more conspicuous in *C. affinis*. Now the oozing out of such a film of wax and the extension of the sperm from the suture over the annulus is what

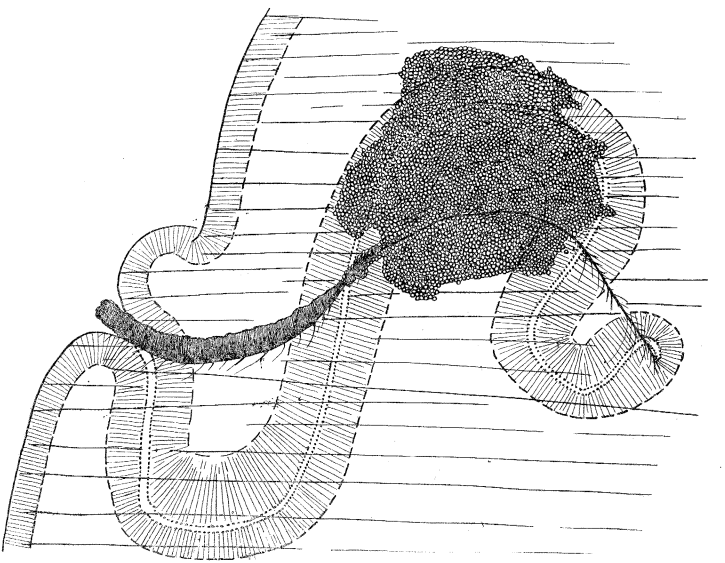

FIG. 10.

was made out, with difficulty, in the specialized annulus of *C. affinis* when mechanical pressure was exerted upon the annulus by forcing the hard sternum of the last thoracic somite against the annulus.

In these *C. montezumæ* the sperm may have been forced out of the pocket by the shrinkage due to the heat with which they were probably killed, or the issuance of sperm may have been a normally produced act in females about to lay and in that case the efficiency of the spine upon the sternum of the fifth legs (Fig. 1) as a means of squeezing the annulus against the sterna in front of it, seems to support the view that it is such spontaneous pressure on the part of the female that liberates the sperm at the right time to meet the eggs.

Comparing the annulus of *Cambarus montezumæ* with that of other Cambari we see that though it departs so much in general form yet it agrees in containing a sperm pocket that is both in structure and use fundamentally identical with the sperm pockets of other Cambari. In all cases known the male fills the inner curves of the pocket with sperm and the outermost curve, near the end into which the male pleopod is thrust, with a wax or cement that seals the sperm in.

The sperm pocket here described is strikingly like that previously described for *C. immunis* (9), both in the simplicity and form of its bendings and in the fact that it runs transversely instead of longitudinally as in most crayfish. Again the form of the pocket here described agrees closely with that of *C. clarkii* (9) though the latter is a longitudinal, median pocket.

The sperm pocket of *C. montezumæ* thus resembles the simplest sperm pockets known, those most like an early stage of the more specialized pocket of *C. affinis*, whose ontogeny has been described elsewhere (10).

As far as the sperm pocket is of any value in indicating phylogenetic affinity it points to the conclusion that *C. montezumæ* is not a highly specialized form, but need not be taken to mean that there is any close relation between *C. montezumæ* and either *C. immunis* or *C. clarkii*, which other characters indicate are remote. And the value of similarity in form of the sperm pockets in these three is nullified by their different positions on the annulus. The ontogeny of the sperm pocket in *C. affinis* shows that it starts as a median groove which secondarily has added to it the part right or left of the median line and if this is the general rule for other Cambari such wide departure from the median position as that in *C. immunis* and *C. montezumæ* may well mean remote connection with such a median form as that in *C. clarkii* and if the ontogeny of the annulus in *C. montezumæ* were known the close resemblance of its sperm pocket to that of *C. immunis* might prove to be a superficial one.

As yet of the six subgenera into which *Cambarus* has been divided by Ortmann the sperm pocket has been made known in four: in *C. affinis*, *C. virilis*, *C. immunis*, representing the subgenus *Faxonius;* in *C. bartoni*, representing the subgenus *Bar-*

tonius; in *C. clarkii*, representing the subgenus *Cambarus* and in *C. montezumæ*, representing the subgenus *Cambarellus*. It would thus be premature to use the facts known as to the sperm receptacle as a guide where they may clash with other criteria for determining the history of the group.

Observations upon the sperm pockets of the two other subgenera, *Paracambarus* and *Procambarus*, both well represented in Mexico, are to be desired.

BALTIMORE, December 1, 1907.

EXPLANATION OF FIGURES.

Figures are all drawn with camera lucida and the Zeiss lenses indicated: Fig. 1 with 2.90 mm.; Figs. 2, 3, 4, 5, 6, 8 with 2A.; Figs. 7, 9, 10 with 2D.; and reduced to ⅓ diameter in Fig. 10 and ½ in the others.

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